MALACOLOGIA, 2009, 51(1): 29–38

LIFE HISTORIES AND DYNAMICS OF STREAM AND LACUSTRINE POPULATIONS OF *MUSCULIUM ARGENTINUM* (D'ORBIGNY, 1842) (BIVALVIA: SPHAERIIDAE) FROM SOUTHERN CHILE

Santiago Peredo*, Esperanza Parada & Pedro Jara-Seguel

Escuela de Ciencias Ambientales, Facultad de Recursos Naturales,
Universidad Católica de Temuco, Casilla 15-D, Temuco, Chile

ABSTRACT

Life histories and population dynamics of two populations of *Musculium argentinum*, one inhabiting a fluvial environment and the other a lacustrine one, are compared. *Musculium argentinum* is oviparous, iteroparous, and sequential incubator, reproducing throughout the year. The life cycle pattern of the fluvial population, unlike the lacustrine one, is characterized by seasonal reproductive variations, more marked in spring and summer, higher fertility and population reproductive productivity (potential recruitment), higher number of marsupial sacs per hemibranch, and smaller size of first reproduction. The content of organic matter and water flow would be the main factors determining the higher population density observed in the fluvial population.

Key words: *Musculium*, Sphaeriidae, population dynamics, freshwater bivalves, Chile.

INTRODUCTION

Sphaeriid clams have a cosmopolitan distribution in a variety of temporary and permanent fluvial and lacustrine freshwater environments (Way & Wissing, 1982). This ubiquity is due to life-history traits involving strategies that allow its permanence, in time and space, in highly unpredictable environments, including the simultaneous hermaphrodite condition, with the possibility of self-fertilization, which allows them to colonize and maintain populations in temporary freshwater bodies (Hornbach et al., 1980, 1982, 1990; Morton, 1985; Hornbach & Childers, 1986; Way, 1988).

Both iteroparity and semelparity are known, with lifespans usually between five and 24 months. In addition, intra- and interspecific variations in brood size are known, yet rarely has an explanation for these variations in life-history and reproductive potential been advanced (Mackie et al., 1976a, b; Mackie, 1978, 1979).

In Chile, sphaeriids are represented by three genera and 11 species: *Psidium* with seven species, *Sphaerium* with two species, and *Musculium* with two species (Parada & Peredo, 2002). The presence of *Musculium argentinum* (d'Orbigny, 1842) in Chile was reported for the first time by Sobarzo et al. (2002) in the Cautín River basin; Parada et al. (manuscript under review) report that *M. argentinum* is found discontinuously in Chile between 38–41°S and 71–72°W, inhabiting streams and lacustrine environments. Recently, Peredo et al. (2007) reported on population dynamics and reproduction of *Musculium argentinum* from a lotic environment. To date, the population dynamics and reproductive traits of lacustrine populations of *M. argentinum* have not been described. In the present paper, a comparative study of life histories and population dynamics of stream and lacustrine populations of *M. argentinum* from humid environments in southern Chile is reported.

MATERIALS AND METHODS

Study Sites

The present study was carried out in two sites with different environmental conditions:

(1) Lautaro stream, (L) corresponds to the evacuation system of Lautaro Fish Farm located in the central valley of southern central Chile (38°32'S, 72°27'W), at 190 m altitude; it runs to the interior of a recreation park with abundant tree vegetation, represented by *Pinus radiata* (D. Don); *Acacia melanoxylon* (R. Br.),

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*Corresponding author: speredo@uct.cl

Eucalyptus globulus (Labill), *Rubus ulmifolius* (Schott), and riverside vegetation, with predominance of *Leontodon taraxacoides* (Vill) Merat, *Plantago lanceolata* (L.), *Taraxacum officinalis* (Weber), and *Blechnum hastatum* (Kaulf). With about 2 km longitude and a mean width of 2 m, the stream flows into the Cautín River.

(2) Lake Villarrica (39°16'27"S, 71°58'54"W) in the Andes foothills, at 250 m altitude. This lake, of glacial origin, has been characterized as oligotrophic, temperate, monomictic, with winter circulation and summer stagnation (Campos et al., 1983). Mean winter temperature is 9.5°C, with minor variations between surface and bottom. The maximum temperatures recorded in spring summer reached 22°C in the epilimnion and 9.5°C in the hypolimnion. The chemical and physical water parameters as well as the phyto- and zooplankton assemblages show marked seasonal variation. *Musculium argentinum* inhabits the coastal area of La Poza Bay (LPB), at the northeast corner of the lake, an area with vegetation of *Juncus procerus* (E. Meyer) and *Salix viminalis* (L.) and with high anthropic influence during the summer.

Biological Parameters

From October 2006 to October 2007, the two studied populations of *M. argentinum* were sampled monthly. The biological material collected (70 specimens per month) was transferred to the laboratory to measure the shell length (SL) of each specimen using a digital caliper. Twenty specimens of known SL were selected at random to determine the presence and number of brooding sacs within inner hemibranchs, number of embryos per sac, and number of extramarsupial embryos. In October 2006, at each location, population density was calculated with ten 400 cm^2 random samples of substratum. Each sample was sifted through 1 mm mesh sieve and specimens in each sample counted. Results are expressed as ind/m^2. Population size structure was determined by analyzing monthly size frequency distributions; size (= age) of first brood was determined at individual and population level. Due to climatic reasons, it was not possible to carry out the sampling in July at LPB. Spearman coefficient (r_S) was used to observe correlation between shell length (SL) and number of brooding sacs present in gravid adults.

Physical and Chemical Parameters of Water and Substratum

In October 2006, at each location, water samples were taken to determine total suspended solids, dissolved oxygen, total alkalinity, pH, total ammonium, nitrate, chloride, calcium, phosphorus, and conductivity. Water samples were processed according to the methodology established by APHA et al. (1992). The flow and depth of the channel and the monthly temperature of water were determined in situ.

To determine the granulometric characteristics and percentage of organic matter in the substrate, in October 2006, at each location, four additional samples of substratum (volume = 800 cc) were

TABLE 1: Population and reproductive parameters of *M. argentinum* stream and lake population and water temperature during the study period.

Parameters	Lautaro Stream population	La Poza Bay Lake population
Maximun shell length (mm)	8.0	7.8
Density (ind/m^2)	325.0	187.5
Maximun individual Fertility	26	18
Mean annual Productivity	96 ± 39	78 ± 25
Maximun number of brooding sac per gill	26	18
Maximun number of embryos per sac	3	2
Mean annual embryos	77.2 ± 15.7	64.9 ± 19.4
Mean annual extramarsupial embryos	19.0 ± 15.3	13.1 ± 10.5
Individual size first reproduction (mm)	2.3	2.8
Mean annual water temperature (°C)	10.6	15.1

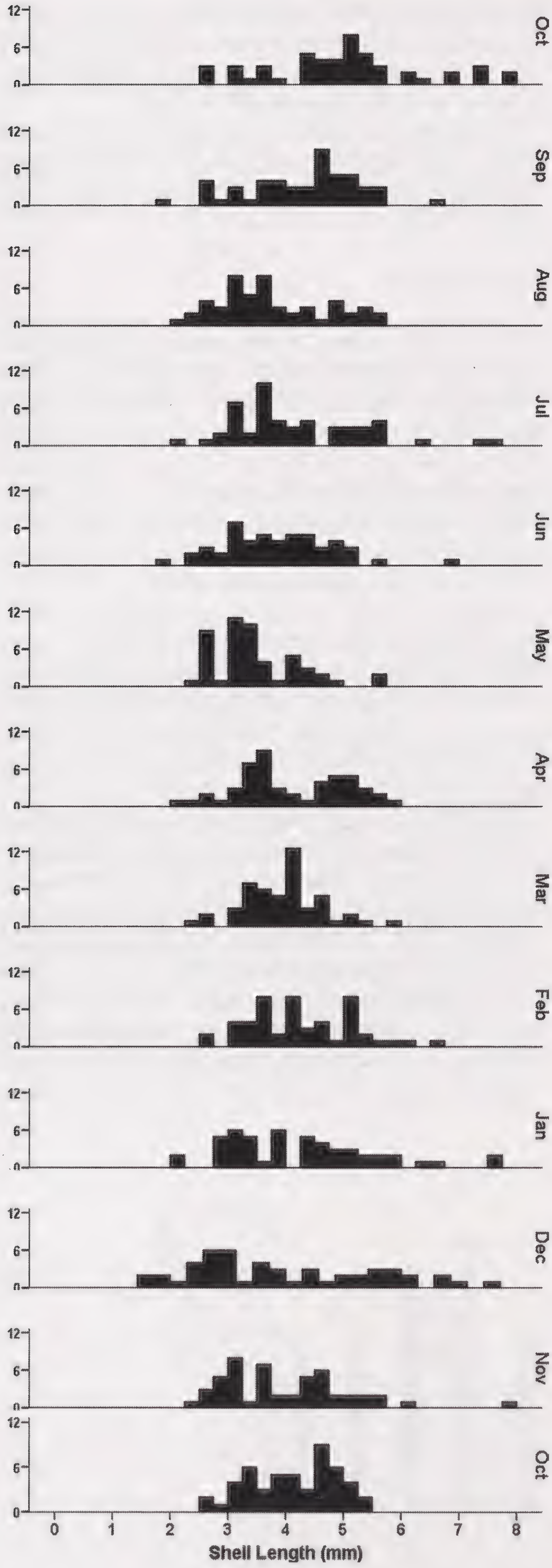

FIG. 1. Monthly size structure of *Musculium argentinum* population at Lautaro stream.

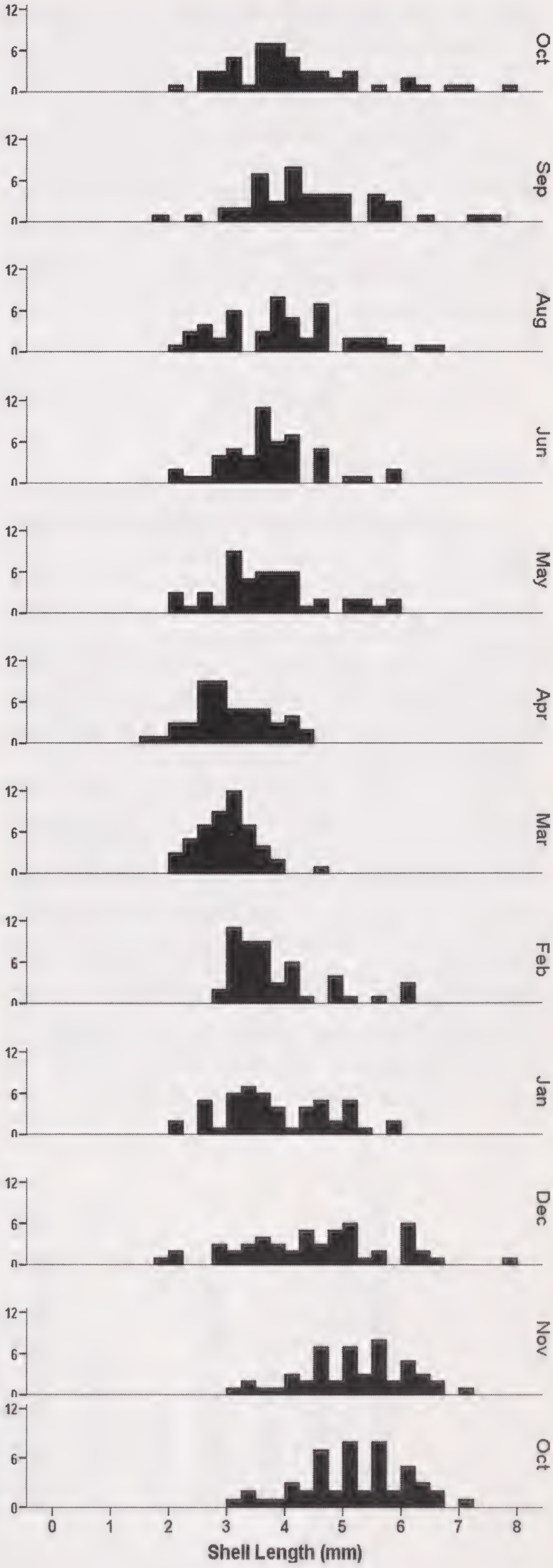

FIG. 2. Monthly size structure of *Musculium argentinum* population at La Poza Bay.

taken. In the laboratory, samples were dried in a Memert oven for 48 h at 110°C. Afterwards each sample was weighed before and after being maintained in a muffle at 500°C for five h to determine content of organic matter. Each substratum sample was sieved through a series of 0.787 mm, 0.278 mm, and 0.083 mm sieves to separate fractions of sand, mud and clay. Differences in granulometry of sampling station substrata were determined according the Textural Triangle (USDA, 1975).

RESULTS

Population Dynamics

From a total of 840 specimens from the lake population, the smallest individual (SL = 1.8 mm) was recorded in December and the largest specimen (SL = 7.8 mm) was recorded in October 2007. In the stream population from a total of 840 specimens collected, the smallest individual (SL = 1.8 mm) was recorded in September and the largest (SL = 8.0 mm) was recorded in October 2006 (Table 1).

Figures 1 and 2 show the monthly size structures of stream and lake populations. Both populations showed similar monthly size-frequency distributions. In the stream populations, the widest size-classes interval appeared in October 2007, whereas in the lake population they appeared in December. Juveniles (specimens with SL of 1.0–1.9 mm) were present throughout the year, being more abundant in the lake population. Figure 2 shows that in the lake population December 2006 and April and September 2007 are the months with the highest number of juveniles, whereas for the stream population the highest number of juveniles were in June and September 2007 (Fig.1).

Population density of *M. argentinum* in the stream population was 325 ind/m^2. On the other hand, the lake population density was 187.5 ind/m^2 (Table 1).

Reproduction

During the spring and summer months, the monthly variation in the number of gravid individuals showed a similar pattern in both populations, that is, a progressive increase in the number of gravid individuals, reaching a peak in January, to decrease towards March, when the lowest values were found. During fall and winter seasons, the reproductive behavior of each population was different: the lake population tends to reach the mean percentage in May, June, August and September over 50% of gravid individuals. Instead, during the fall months, the stream population showed a percentage of gravid individuals below 40%, with an increase in July and a decrease in September (Fig. 3).

Adults with brooding sacs were present throughout the year in both populations. However, extramarsupial embryos were not recorded in November and August for stream population samples, and in January, February and July in the lake population samples. The stream population showed gravid individuals with up to three sacs per demibranch during December and October. In the lake population, the maximum number of brood sacs per hemibranch was

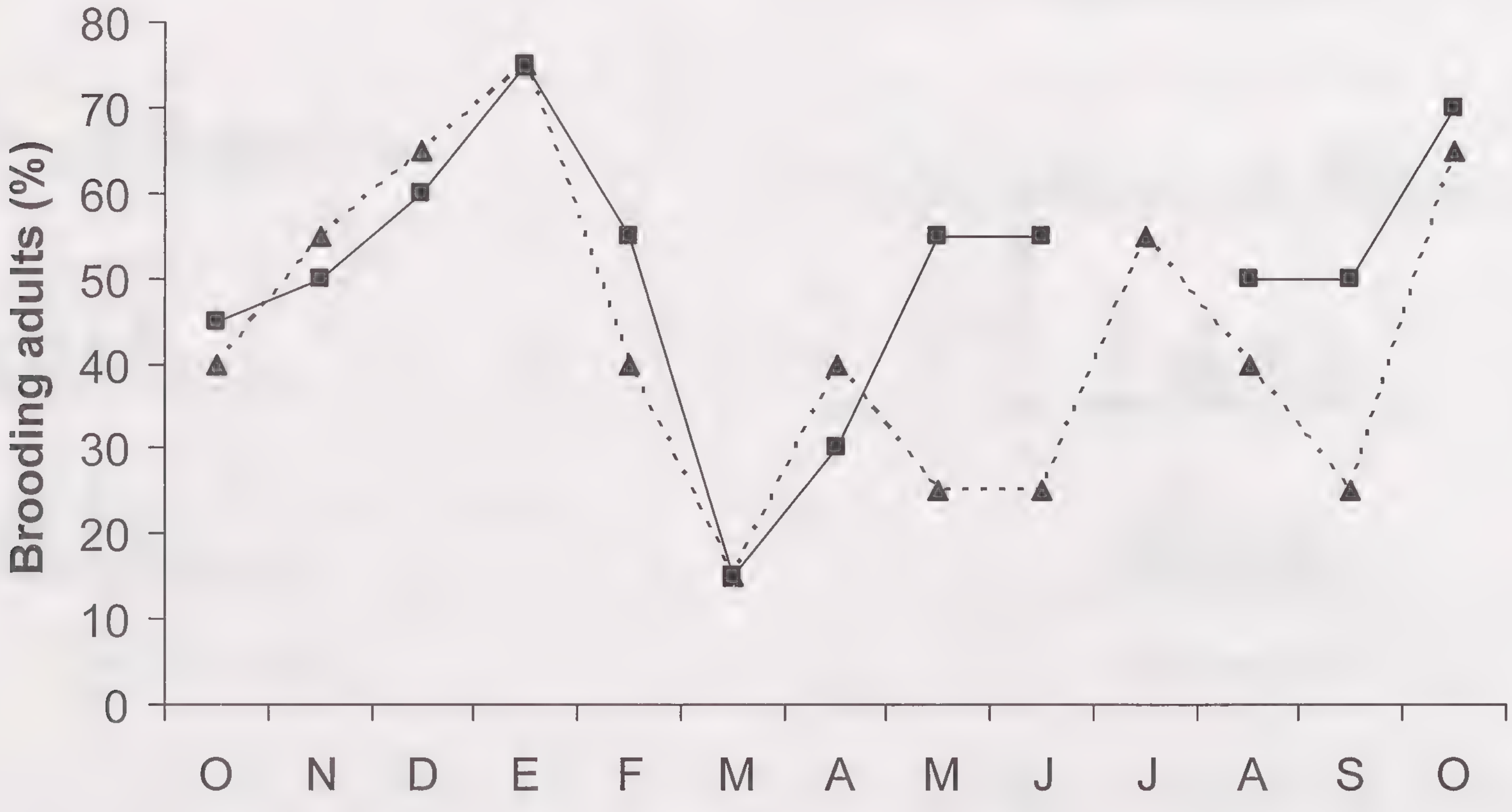

FIG. 3. Monthly variation of the percentage of gravid specimens at Lautaro (triangles) and La Poza Bay (squares) populations.

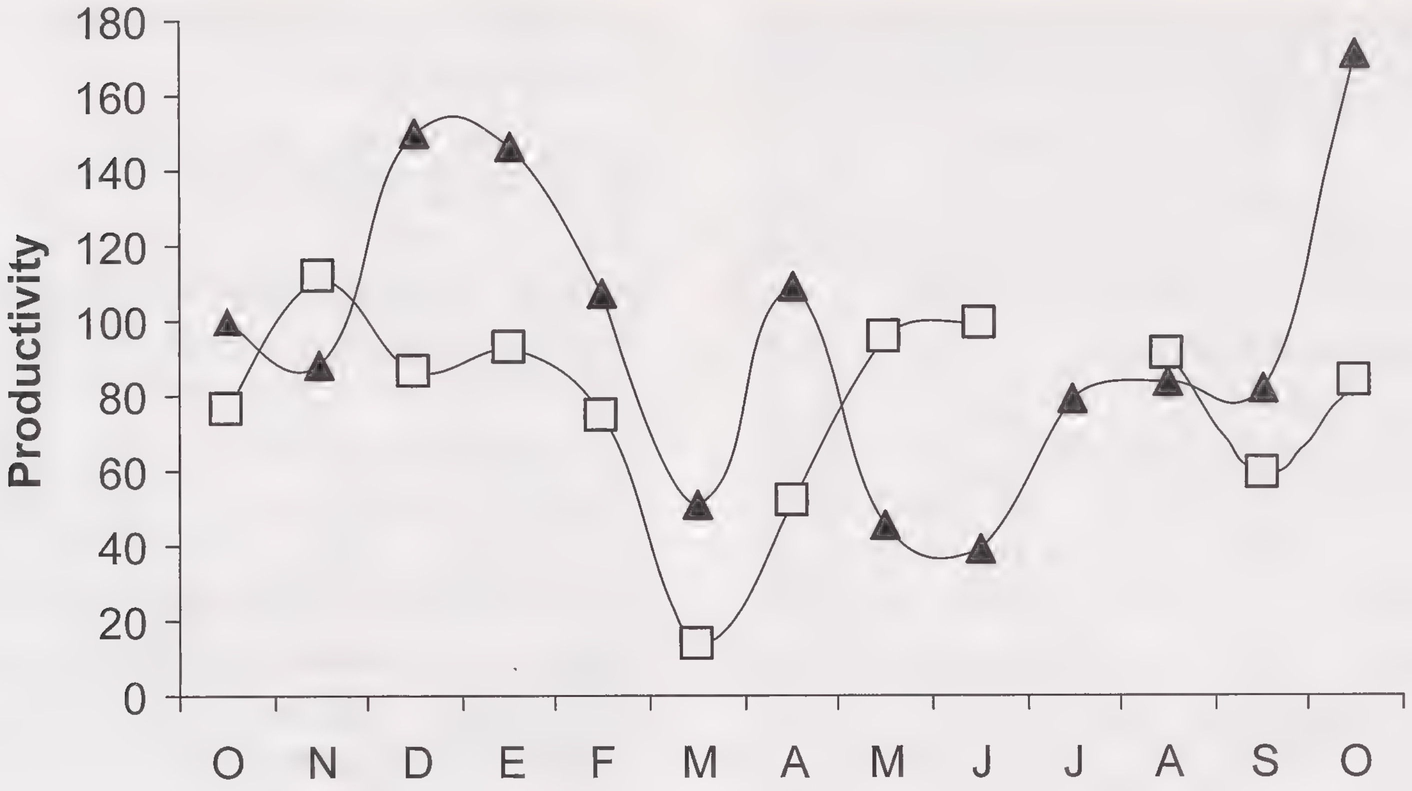

FIG. 4. Monthly potential productivity (number of within-sac embryos plus extramarsupial embryos) in Lautaro (stream) (triangles) and La Poza Bay (lake) (squares) populations.

two (Table 1). In both populations, there is a low positive, significant (P = 0.001) correlation between SL and number of brood sacs in gravid adults (L $r_s = 0.48$; LPB $r_s = 0.31$).

The mean values of annual productivity (or potential recruitment) measured as the number of embryos contained in brood sacs and extramarsupial embryos within the suprabranchial chamber produced by adults was: 96.2 ± 39 embryos in the stream population and 78 ± 25 for the lake population (Table 1). Monthly variations of this parameter for the populations under study are shown in Figure 4. Although both populations showed a similar tendency throughout the year, values of potential recruitment for the stream population were consistently higher that those corresponding to the lake population, with the exception of May and June, when the productivity in stream population was lower. At the individual level, monthly variations of maximum individual fertility (measured as the number of intra- and extramarsupial embryos produced by a single individual) in each population are shown in Figure 5. The stream population showed the highest values, 26 embryos, in April and October, corresponding to maternal individuals of 4.5 mm and 6.2 mm SL respectively. In the lake population, the highest value of fertility was 18 embryos in January for a maternal individual of 4.7 mm SL (Table 1).

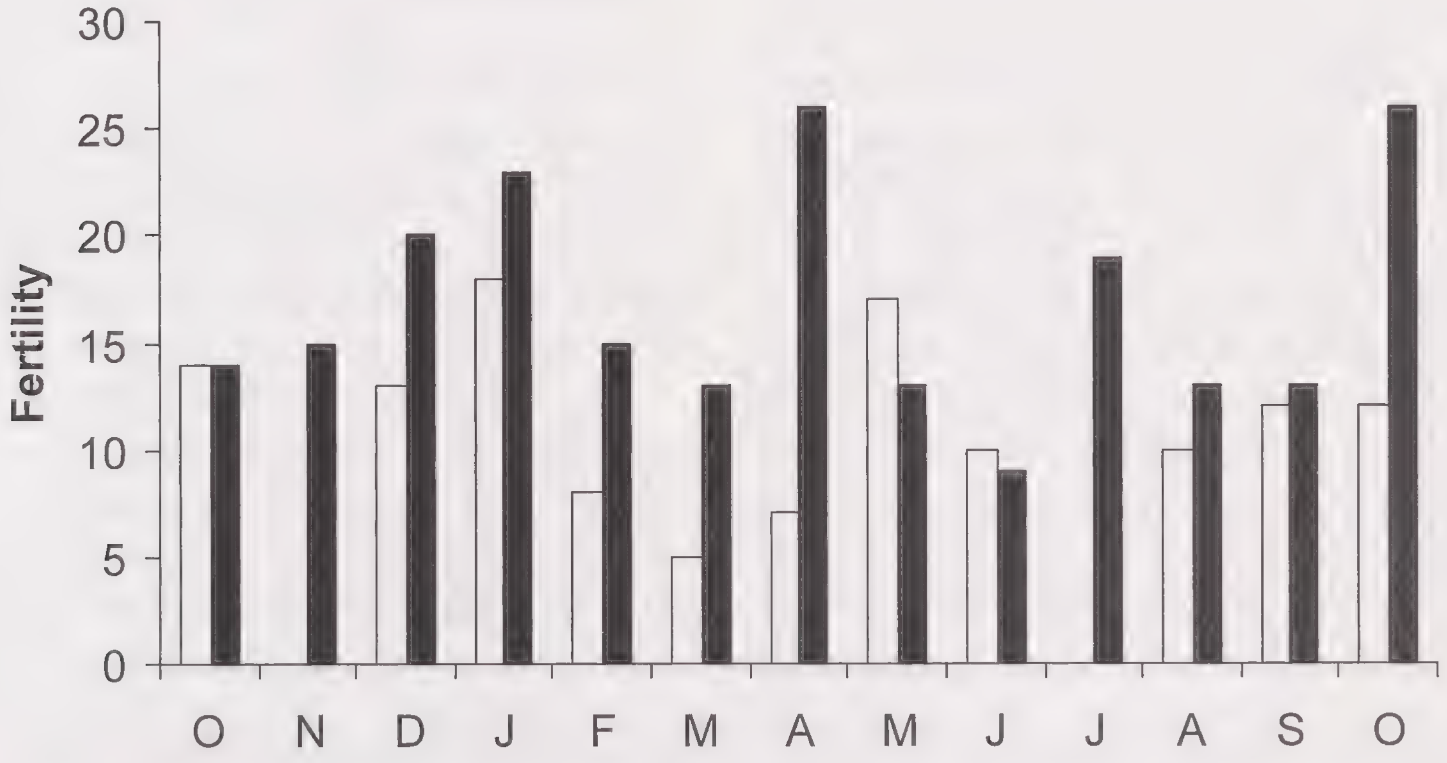

FIG. 5. Monthly variation of highest individual fertility (specimen with the highest number of within-sac embryos and extramarsupial embryos) in Lautaro (stream) (black) and La Poza Bay (lake) (white) populations.

TABLE 2: Water physical-chemical parameters at Lautaro and La Poza Bay sampling stations during the study period.

Parameters	Lautaro	La Poza
Total suspended solids (mg/l)	1.5	1.6
Conductivity (µS/cm)	62.1	57.9
Dissolved oxygen (mg/l)	11.54	10.13
pH	7.71	7.79
Alkalinity (mg/l)	26.50	28.35
Calcium (mg/l)	5.73	0
Total ammonium (mg/l)	0.024	0.007
Nitrite (mg/l)	0.003	0.050
Nitrate (mg/l)	0.06	0.06
Chloride (mg/l)	0.7	1.3
Phosphorus (mg/l)	0.03	0.01
Sulphate (mg/l)	0	6
Temperature (ºC)	10	13
Deep (cm)	15.7	30.0
Water flow (m/s)	55	0

Table 2 shows the minimum size of brooding individuals of *M. argentinum* obtained monthly for each population. The results show that the smallest gravid individual in the stream population was 2.3 mm SL and in the lake population 2.8 mm SL, collected in May (Table 1). The size of first brooding at the population level varied seasonally. The smallest size class for which 50% of individuals were gravid corresponded in both populations to the size class of 3.0–3.9 mm recorded in August and July for the stream population and in February and May for the lake population.

Habitat Characteristics

The physical and chemical characteristics of the substratum at each study site showed differences in the organic matter content and granulometry. At the stream station, the substratum had a considerably higher percentage of organic matter (11%) than the lake station with only 1.5%. Both stations also showed differences in granulometry. At the stream, the substratum was predominantly mud and clay, with 0.91% of sand (54% of mud and 45.1 of clay); at the lake, a clay fraction as dominant (81%), with 7.3% of sand and 12.2% of mud.

Table 2 shows the other physical and chemical parameters at lake and stream. The water quality of both habitats is similar with differences in the values corresponding to chloride and nitrite, particularly at the lake, where differences are more marked. Ammonia and phosphorous levels are 3–4 times higher in the stream than the lake. Calcium was only present at the stream. Differences between the habitats are great, especially due to the depth fluctuations in the coastal areas of Lake Villarrica, reaching the minimum, 30 cm, in summer and a maximum of 2.5 m in winter; the lake is also characterized by the lack of water circulation, in contrast with the stream, where the water flow is 0.5 m/s, without significant variations throughout the year. Monthly variations of water temperature in the habitats showed the same tendency throughout the year, however, at the stream, temperatures were consistently lower (Fig. 6).

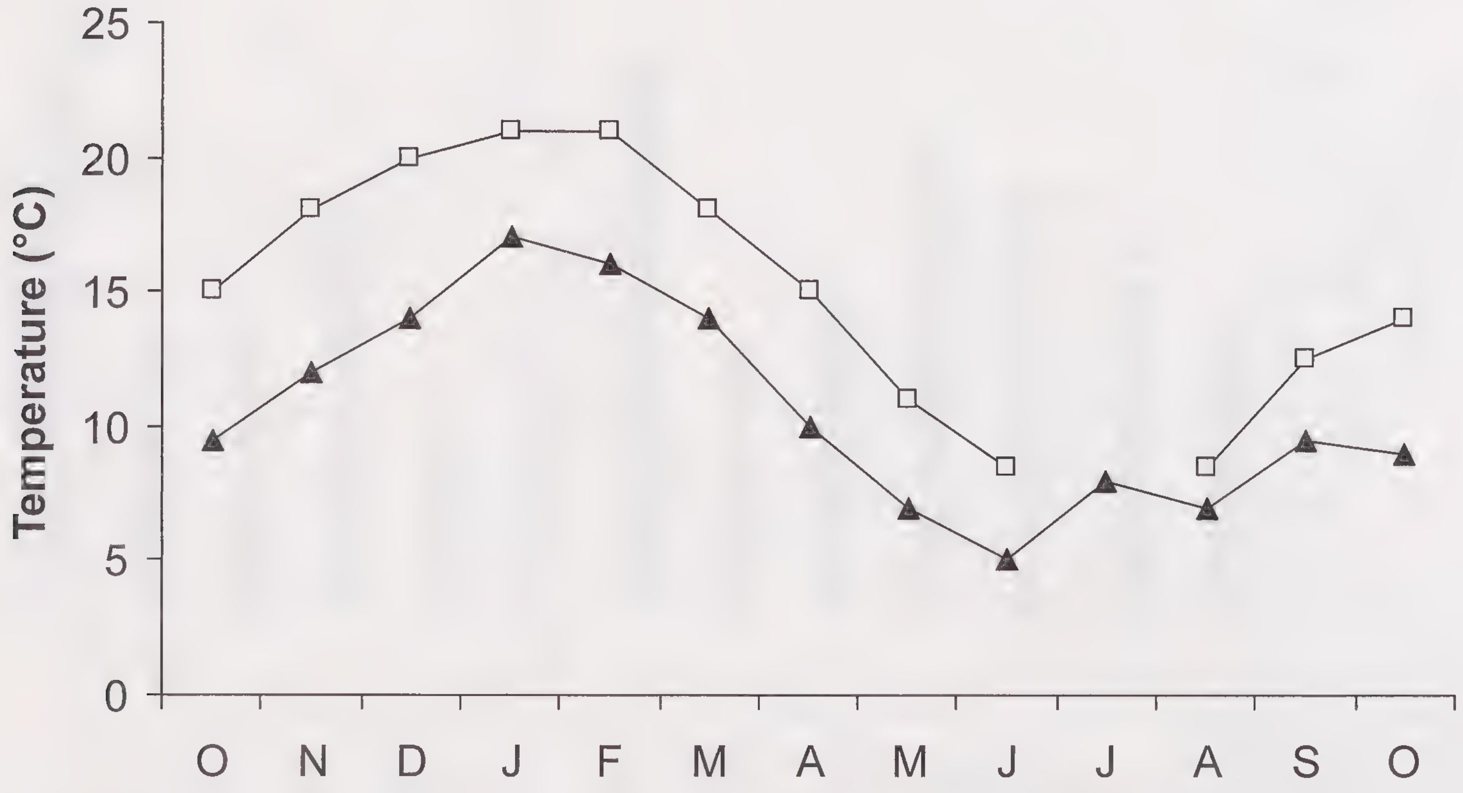

FIG. 6. Monthly water temperature at Lautaro (triangles) and La Poza (squares) during the study period.

DISCUSSION

All individual experience environmental variations in abiotic or biotic conditions. Such environmental variation has a strong impact on the fitness of individuals and thus strongly influences the evolution of life-histories strategies.

The present study of the life histories of stream and lacustrine populations of *M. argentinum* showed a similar pattern in the annual variation of the size-frequency distributions; brooding was observed in a broad interval of size classes (2.3 to 8.0 mm SL) throughout the year. *Musculium argentinum* is an ovoviviparous, iteroparous, and sequential brooder. These results correspond to those reported by Peredo et al. (2007) for *M. argentinum* in other localities of southern Chile. Iteroparity in *M argentinum* populations could be indicative of a strategy to favor reproductive success, as indicated by numerous models (Wilbur & Rudolf, 2006) Nevertheless, some substantial differences between stream and lacustrine populations were observed (Table 1). Although in both populations incubation and recruitment were recorded throughout the year, the stream population showed a more defined seasonal variation in the annual reproduction, with higher values in the frequency of gravid individuals in spring and summer (October to February, with a maximum in January) and a noticeable decrease in fall and winter (Fig. 3). In contrast, a more uniform brooding behavior throughout the year was observed in the lake population, for which only one noticeable decrease in the number of gravid specimens was observed in March, with a relative stable number of gravid adults during the rest of the year.

Furthermore, specimens from the stream population showed within each size class a higher number of embryos contained in brood sacs and extramarsupial embryos, which explains the higher values of individual fertility and productivity or potential recruitment observed in the stream population (Figs. 4, 5).

Specimens of from the stream population produced up to three brood sacs per hemibranch; instead, the maximum number of sacs per demibranch in the lake population was two (Table 1). In both populations, there was low positive, significant (P = 0.001) correlation between the number of sacs produced and shell length of maternal specimens, a fact reported by Peredo et al. (2007). Beekly & Hornbach (2004) reported that in *Sphaerium striatinum* (Lamarck, 1818) the brood size is limited by two general constraints, the marsupial sac and the retention of extramarsupial offspring. In our study, specimens from the stream population, in which the maximum number of brood sacs/demibranch was higher, showed higher values in the convexity index or shell roundness (sensu Ituarte, 1996) (65.4 for the stream and 59.1 for the lake) (Parada et al., under revision). This means that, compared with the lake population, the stream population specimens have more globose shells; this morphometric characteristic is directly related to a larger mantle cavity volume, a factor that would result in a higher capacity for lodging offspring.

Another difference between stream and lake populations was found in the smallest size at which an individual is ready for brooding; 2.3 mm SL in the stream population and 2.8 mm in the lake population (Table 1). In both populations, the smallest gravid individuals were observed in May. This suggests that specimens from stream population reached mature reproductive condition earlier than those from lake population.

Mackie et al. (1976) reported that inter- and intrapopulation variations in the fertility of *Musculium securis* (Prime, 1852) could be explained by differential mortality of embryos during the incubation period. This was not the case *of M. argentinum* populations studied here, in which all dissected brood sacs observed monthly, dead embryos or remains of dead embryos were never found. There are no reports that embryo mortality in *Musculium* can be attributed to development retention to provide nutrition to other embryos, as reported in marine mollusks (Gallardo & Garrido, 1987).

The themes of density-dependent regulation, resource availability, and environmental fluctuations are integral to current demographic theory and are potentially important in any natural system (Reznick et al., 2002). The interpopulation differences in fertility recorded in *M. argentinum* could be explained rather as a response to differences in habitat characteristics. Differences in food supply represented by the significantly higher quantity of organic matter available for the stream population (11%) versus 1.5% in the lake population in the sediment used as food could be a factor that could influence fertility and productivity. The higher fertility recorded in the stream population could be advantageous to compensate for the loss of juveniles swept away by the water current (Parada et al., under review). The importance of the organic matter in the sediment has been documented for *M. lacustre* (Müller, 1774) (Morton, 1985;

Mouthon, 2004) for *M. securis* by Mackie et al. (1976a) and for *Sphaerium striatinum* by Raikow & Hamilton (2001).

Reproductive traits shown by both populations (gravid adults throughout the year) do not allow determination of the reproductive effort per year. According to Mackie (1979), *M. argentinum* has a continuous food supply and energy allocated mainly to reproduction.

Many authors, empirically as well as theoretically, have tried to correlate life-history traits of different species – age of the first reproduction, fertility, iteroparity or semelparity, growth rate, and generational time, amongst others – with habitat characteristics (MacArthur, 1960; Cody, 1966; Pianka, 1970; Southwood et al., 1974; Wilbur et al., 1974; Stearns, 1976; Parada et al., 1990; Parada & Peredo, 1994).

Population densities of *M. argentinum* at the stream and the lake showed marked differences: 325 ind/m^2 and 187.5 ind/m^2, respectively. In this context, the environmental parameters represent relevant factors in the dynamics, reproductive biology, and permanence of populations in time. It is just as a conjunction of parameters are observed in common where the populations of *M. argentinum* are located; the water registers maximum averages of 23°C and minimum of 8°C, low values of total dissolved solids, low conductivity, waters highly oxygenated and, neuter pH, with low values of ammonium, nitrite, nitrate chloride, sulphate, inorganic phosphorus, and calcium, and differences in organic matter content in the substratum (Table 3). These values are much lower than those recorded in Saone River in France for *Musculium lacustre* (Mouthon, 2004). The studied populations of *M. argentinum* occur in water bodies with clay (lake population) or clay- muddy bottoms (stream population), with organic matter contents ranging from 11.03 to 1.52% for L and LPB respectively. From the above mentioned environmental parameters, content of organic matter and water flow would be the main factors determining the higher population density observed in the stream population.

The low or absent calcium in Lautaro stream and La Poza Bay water is remarkable. Burky et al. (1979) suggested that sphaeriid clams have a common strategy for shell secretion that is presumably under genetic control. Energetically, it would seem most economical for clams to build the most calcareous shell in the hardest water or the most proteinaceous shells under the most eutrophic conditions. However, in terms of water hardness, this hypothesis must be rejected since interspecifically there is no relationship between shell calcium and water hardness, and there is an inverse relationship for *Sphaerium striatinum.*

Although no water characteristic can explain the relationship between the calcareous and organic components of shell, trophic conditions give the best explanation at the generic level, because *Musculium* is at the opposite end of the eutrophic scale from all other sphaeriids that have been examined. The inverse relationship between the amount of shell calcification and water hardness for *S. striatitum* is indicative of selection for other patterns of shell secretion at the species level. At the same time, data on populations of *Musculium*, *Sphaerium* and *Pisidium* suggest selection for shell of a base level of adaptative need and mechanical function (inverse relation between shell organic and shell $CaCO_3$) before the splitting of the Sphaeriidae into genera.

The *Musculium argentinum* studied inhabit soft waters and with absence or very low calcium concentration. The physical-chemical parameters of the water where *M. argentinum* populations live corresponds to an oligotrophic to mesotrophic environment. However, according to the organic matter recorded in the substratum, especially that present in Lautaro stream, corresponds to a eutrophic environment. *Musculium argentinum* in contrast to *Sphaerium striatinum,* lives in softwater, with low calcium concentration level which does not affect shell formation, thus corroborating Burky et al. (1979) observation with respect to the inverse relationship between the amount of shell calcification for *S. striatinum* being indicative of selection for other patterns of shell secretion at the species level.

Selection for life in variable habitats has evoked speculation about of the deterministic r and K selection theory to life history tactics (Pianka, 1970; Hornbach et al., 1980; McLeod, 1981). Heard (1977) concluded that some sphaeriidae species are r strategists because they produce many young of low energy content and live in variable habitats. In contrast, other species of Sphaeriidae are K strategists, occupying more stable habitats and producing few offspring of high energy content. Results of the present study do not allow characterization of either population as r or K strategists because reproduction traits and environmental conditions do not fit with features of r or K strategies. Hornbach et al. (1980), Way et al. (1980), and McLeod et al. (1981) pointed out that data on *M. partumeium* (Say, 1822) seem to support a bet-hedging strategy. According to our study, *M. argentinum* would also be a bet-hedging strategist, but each population could have its own strategy, as pointed out by Burky (1983).

Musculium argentinum has a wide, discontinuous distribution in southern South America, from southern Brazil (Mansur et al., 1991, Ituarte, 1996) to Montevideo, Uruguay (Figueiras, 1965), and it is widely distributed in Argentina (Ituarte, 1996) and Chile, occupying different biotopes and climates. This species thus is an attractive study-model for the analysis of a variety of ecological and historical circumstances that influence and life histories in different environmental conditions.

ACKNOWLEDGEMENTS

We are grateful to the Dirección General de Investigation, Catholic University of Temuco, Chile (Project 2006-3-12) for financial support.

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Revised ms. accepted 16 October 2008